

## **Memory performance influences male reproductive success in the wild**

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## 1 SUMMARY

2 Despite decades of comparative research, how selection shapes the evolution of  
3 cognitive traits remains poorly understood [1–3]. Several lines of evidence suggest that  
4 natural selection acts on spatial memory in food-caching species [3–6]. However, a link  
5 between reproductive fitness and spatial memory ability has yet to be demonstrated in  
6 any caching species [1,3,7]. Here we show that memory performance influences  
7 reproductive success differentially for males and females in a caching songbird, the  
8 New Zealand robin (*Petroica longipes*). Males' memory performance in a spatial task  
9 during winter influenced their subsequent breeding success; individuals with more  
10 accurate performance produced more fledglings and independent offspring per nesting  
11 attempt. Males with superior memory performance also provided an increased  
12 proportion of large prey items to chicks in the nest and spent less time flying while  
13 foraging and provisioning. No such effects were found for females. Previous research  
14 reveals that trade-offs may constrain selection and act to maintain variation in cognitive  
15 traits [8,9]. The gender dimorphism in the reproductive benefits of robin memory  
16 performance suggests an additional role for divergent selection between the sexes in  
17 constraining runaway selection on male memory ability [10], ultimately maintaining  
18 variation in this cognitive trait.

## 19 KEYWORDS

20 spatial memory; food caching; cognitive evolution; reproductive success; evolutionary  
21 ecology

## 22 RESULTS AND DISCUSSION

23 Individual variation in cognitive performance is well documented across the animal  
24 kingdom [11], yet the ecological and evolutionary significance of cognitive variation is  
25 poorly understood [2,3]. Understanding the evolutionary ecology of cognitive traits  
26 requires examining whether and how selection acts on cognitive traits in the wild [1].  
27 Pioneering studies of the fitness consequences of cognition have primarily examined  
28 the link between reproductive success and problem solving performance [8,12–14] or  
29 the ‘general’ cognitive performance captured by cognitive test batteries [15–17] (but see  
30 [18]). However, making clear predictions about how these broad measures of cognitive  
31 performance (which will presumably underpin a suite of behaviours) should influence  
32 fitness remains challenging [17,19]. To further our understanding of cognitive evolution,  
33 we must therefore target specific cognitive traits [19] underpinning behaviours directly  
34 linked to survival and reproduction in the wild [2,3].

35 Food caching is a well-established study system for investigating the evolution of  
36 spatial memory [20], making caching species excellent candidates for studying the  
37 evolutionary ecology of a specific cognitive trait [1,3]. There is intraspecific evidence  
38 that spatial memory and its neural correlates can undergo fine scale selection in  
39 response to environmental variation. For example, food storing chickadees (*Poecile* sp.)  
40 from harsher, more unpredictable, high altitude environments possess neurological  
41 adaptations and more accurate memory for cache locations compared to conspecifics  
42 from lower altitudes [5,7,21–23]. To date, however, the fitness consequences of  
43 intraspecific variation in spatial memory have not been examined in any caching  
44 species [1,3,7].

45 In the current study we investigate how memory performance in a spatial task  
46 influences reproductive success in a caching songbird, New Zealand’s North Island

47 robin (*Petroica longipes*; hereafter referred to by their Māori name, toutouwai). The  
48 toutouwai is a socially and genetically monogamous [24] forest dwelling species.  
49 Toutouwai regularly consume some of the largest invertebrates on earth [25] and will  
50 cache year round, with a peak in intensity in winter, particularly for males [26]. These  
51 bold and curious birds are highly territorial; traits that make wild, free living individuals  
52 amenable to cognitive testing across a range of domains [27–29], as well as easily  
53 monitored during the breeding season [30]. During the austral winter (June 2016) we  
54 measured individuals' ( $N_{male} = 36$ ,  $N_{female} = 27$ ) performance in an associative-learning  
55 task where a spatial cue signalled the presence of a reward [31]. We hid a mealworm  
56 inside one of eight compartments in a circular apparatus (Figure 1 A). Each toutouwai  
57 was tested once in the experiment: we gave the apparatus to a bird several times in a  
58 single day, always at the same location within their territory, with the reward concealed  
59 in the same compartment, such that it was in a consistent location relative to territory  
60 landmarks across all trials (Figure 1A). Toutouwai cache their invertebrate prey over  
61 short time intervals [25,32], we therefore used an ecologically relevant delay interval of  
62 one hour between trials in our spatial memory experiment (the experiment consisted of  
63 an initial probe and consolidation trial, followed by four separate test trials, ending with  
64 a control trial).

65 Spatially based associative-learning tasks can provide a measure of spatial  
66 memory performance [31]; individuals who remember the correct location and quickly  
67 form an association between the spatial cues and reward will open the fewest lids  
68 during test trials. Toutouwai learned the specific location of the food reward, as they  
69 opened fewer compartment lids to retrieve it over the course of the trials (Figure 1B;  
70 GLMM trial coefficient estimate, CE = -0.064, 95% confidence interval, CI = -0.103 to  
71 -0.026; also see Table S1). There was moderate individual consistency in memory

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74 performance over time, as there was repeatability in the number of lids that an  
75 individual opened across their test trials (when statistically controlling for the influence  
76 of trial sequence [33],  $R_{adjusted} \pm SE = 0.199 \pm 0.062$ ,  $P = 0.0001$ , 95% CI = 0.046 to  
77 0.295). This moderate repeatability estimate for toutouwai memory performance is  
78 consistent with repeatability estimates for cognitive performance in a range of non-  
79 human species [34]. To examine the link between reproductive success and spatial  
80 memory we quantified individual memory performance as the total number of lids  
81 opened during the four test trials (following the methods of [35,36]). We investigated  
82 whether this memory performance measure was influenced by possible confounds;  
83 there was no effect of age, body condition or sex on individual memory performance  
84 (GLM: body condition CE = 1.345, 95% CI = -0.671 to 3.397; Cohort CE = 0.032, 95%  
85 CI = -0.016 to 0.082; Sex CE = -0.041, 95% CI = -0.240 to 0.161).

86       To examine whether memory performance influenced an individual's subsequent  
87 reproductive success we monitored all test subjects that remained in the study area  
88 during the following breeding season (September 2016 – March 2017;  $N_{males} = 31$ ,  
89  $N_{females} = 18$ ) and used a multi-model averaging approach [37], controlling for life history  
90 traits. Table 1 provides the factors that were included in these models; we ran all  
91 possible models based on combinations of these predictors and calculated estimates  
92 for model parameters by averaging across models (as none of the top candidate  
93 models were clearly the best fit, i.e.  $AIC_w \geq 0.9$ , see Table S2) [37,38]. Individual  
94 memory performance did not affect the reproductive success of either sex in the earlier  
95 stages of nesting (i.e. season start date, the number of clutches laid and hatching  
96 success; see Table S3). However, spatial memory performance influenced male, but  
97 not female reproductive success during the later stages of each breeding attempt  
98 (Figures 2A-D; Table S3). Compared to males with poor spatial task performance,

99 males with superior memory performance fledged more chicks per clutch ( $N_{nests} = 54$ ;  
100 mean  $\beta \pm SE = -0.075 \pm 0.035$ , 95% CI = -0.146 to -0.003; Figure 2A) and produced  
101 more independent offspring per clutch (i.e. independently foraging and beginning to  
102 disperse [39];  $N_{nests} = 54$ ; mean  $\beta \pm SE = -0.071 \pm 0.032$ , 95% CI = -0.135 to -0.006;  
103 Figure 2C), but only tended to produce more independent offspring over the whole  
104 season ( $N_{males} = 31$ ; mean  $\beta \pm SE = -0.052 \pm 0.30$ , 95% CI = -0.113 to 0.010). While our  
105 analyses controlled for several potential determinants of toutouwai reproductive  
106 success (see Table 1), without experimental manipulation we cannot completely  
107 exclude the possibility that memory performance covaried with unexamined ecological  
108 or life history factors [8]. Nonetheless, this evidence that memory performance in a  
109 spatial context is associated with reproductive success in the wild supports the  
110 prediction that spatial memory is likely to be under directional selection in food-caching  
111 species [2].

112       Cognition is only visible to selection via ecologically relevant behavioural  
113 variation [3]. In a toutouwai pair the female builds the nest, incubates eggs and broods  
114 chicks, while the male assists in provisioning her until the chicks have hatched, at which  
115 point both sexes provision the young [39]. The brood is divided post fledging, with  
116 males often caring for more young than females and frequently caring for fledglings for  
117 longer periods of time [39]. Thus male provisioning behaviour is likely to make a larger  
118 contribution to the overall success of the later stages of each breeding attempt (i.e. from  
119 post-hatching through to fledgling independence). We observed a pair's foraging and  
120 provisioning behaviour when chicks in the nest were 15-16 days old, fully feathered and  
121 no longer reliant on brooding by the female. We estimated the total mass of food  
122 delivered to each chick per hour (see methods for details). The total mass fed to chicks  
123 increased as parents spent more time foraging (Table S4) and was lower for females

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126 with superior memory performance (mean  $\beta \pm SE = 0.015 \pm 0.006$ , 95% CI = 0.001 to  
 127 0.030). By contrast, there was no effect of male memory performance on the total mass  
 128 of food delivered to chicks (Table S4). However, memory performance influenced a  
 129 male's provisioning strategy. Males with superior memory performance delivered a  
 130 larger proportion of large prey to the nest (Figure 3A; mean  $\beta \pm SE = -0.120 \pm 0.041$ ,  
 131 95% CI = -0.207 to -0.033) and increasing food delivery size was associated with a  
 132 lower provisioning rate (i.e. the number of provisioning trips made per minute spent  
 133 foraging; mean  $\beta \pm SE = -8.915 \pm 3.565$ , 95% CI = -16.456 to -1.373). In sparrow chicks  
 134 (*Passer domesticus*) the provisioning rate of only the largest food items, rather than the  
 135 overall food delivery rate, is associated with increased fledging mass and future  
 136 recruitment [40]. Thus although male toutouwai memory performance did not influence  
 137 the overall provisioning rate, if toutouwai chick growth rates are similarly dependent on  
 138 the provisioning of larger prey items [40], selection may act on male memory via  
 139 provisioning behaviour during the breeding season, by favouring those males that are  
 140 better able to provision larger prey to offspring.

141 We suggest it is likely that our memory task provides a measure of an  
 142 individual's ability to accurately form associations between food rewards and spatial  
 143 cues and/or landmarks. In the context of provisioning, this type of recall may allow birds  
 144 to efficiently locate, process and deliver large prey to chicks on the nest. Some of the  
 145 large invertebrate species in the toutouwai's diet have a clumped diurnal spatial  
 146 distribution (e.g. Wellington tree wētā, *Hemideina crassidens* [41]). Moreover, due to  
 147 their size such prey must be broken into smaller pieces before they can be consumed  
 148 [42]. This activity is usually carried out in a secluded, ground-level location on the  
 149 territory, with pieces then carried to the nest in multiple trips [42,43]. In the context of  
 150 provisioning, accurate memory for spatial or landmark cues may therefore increase

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170 | efficiency of movement between the nest and high value food patches. In the context of  
171 | caching, toutouwai also dismember large prey in the same manner, before moving  
172 | pieces to individual cache sites in the canopy [25,42]. Experimental evidence from  
173 | caching corvid and parid species suggests that accurate cache retrieval is underpinned  
174 | by associations formed between food caches and spatial cues or landmarks [44–47].  
175 | The use of landmarks and spatial cues during cache retrieval has yet to be investigated  
176 | in toutouwai; however, our behavioural observations do provide some putative evidence  
177 | that male memory performance influences provisioning efficiency. Males with superior  
178 | memory performance spent less time flying per hour (Figure 3B; mean  $\beta \pm SE = -0.102$   
179 |  $\pm 0.027$ , 95% CI = -0.159 to -0.045), while this was not the case for females (Table S4).  
180 | For males, flight time was also negatively associated with the proportion of large prey  
181 | delivered to the nest (mean  $\beta \pm SE = -1.692 \pm 0.671$ , 95% CI = -3.131 to -0.253), but  
182 | not with overall provisioning rate (see Table S4). These links cannot be attributed to a  
183 | correlation between territory quality and memory performance, as we found no  
184 | associations between memory performance and foraging rates (Table S4) or breeding  
185 | territory size (median size = 3640 m<sup>2</sup>, range = 1300 – 8340 m<sup>2</sup>; correlation for males:  $R_s$   
186 | = 0.05,  $N = 32$ ,  $P = 0.78$ ; correlation for females  $R_s = -0.28$ ,  $N = 19$ ,  $P = 0.24$ ). Instead,  
187 | these patterns suggest that males with better memory performance are expending less  
188 | energy to provision offspring, both by delivering larger prey to the nest and by reducing  
189 | costly movements within their territory. To further investigate how selection may act on  
190 | memory performance in the context of both provisioning and caching, future research  
191 | should aim to test the links between toutouwai memory performance, natural prey  
192 | search and processing efficiency and the spatial cues used by toutouwai during cache  
193 | retrieval.

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197 Males and females did not differ in their performance in our spatially based  
198 associative-learning task, yet individual variation in cognitive performance influenced  
199 provisioning behaviour and reproductive success differentially for each sex in our study  
200 population. This difference may arise both because female toutouwai typically  
201 contribute less to the overall provisioning of offspring (see above discussion) and  
202 because they are less reliant on their own caches of food at all times of the year,  
203 particularly when they must compete for food with their more dominant mates [48].  
204 When the sexes have different selective optima for shared phenotypic traits, divergent  
205 selection may act to maintain variation within a population [10,49,50]. Our results raise  
206 the possibility that male and female toutouwai differ in terms of their selective optimum  
207 for memory performance. Ultimately, this difference may constrain runaway selection on  
208 male memory ability and contribute to the maintenance of interindividual variation in  
209 spatial memory within the toutouwai population [50]. In addition, as there was only a  
210 tendency for males with more accurate memory performance to produce more  
211 independent young across the whole season, it also remains possible that undetected  
212 costs or life history trade-offs constrain selection on male memory ability in this  
213 population [8]. Our data represents selective processes shaping cognitive variation  
214 within a single season for this relatively long-lived passerine. Nonetheless, it points  
215 towards mechanisms that may maintain individual variation in spatial memory in food-  
216 caching species.

## 217 **SUPPLEMENTAL INFORMATION**

218 Supplemental Information includes 4 tables and the three datasets supporting this  
219 study.

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## 231 **AUTHOR CONTRIBUTIONS**

232 R.C.S., N.S.C. and K.C.B. conceived the study. R.C.S. designed the spatial task  
233 methodology, collected cognitive performance and breeding season data, carried out  
234 analyses and wrote the manuscript. R.D.M collected behavioural observation and  
235 breeding season data. All authors discussed the results and commented on the  
236 manuscript.

## 237 **DECLARATION OF INTERESTS**

238 The authors declare no competing interests.

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382

383 **Figure 1. The experimental set-up (A) and the number of lids opened by**  
384 **toutouwai during the memory test (B).** The dashed line in (B) represents the number  
385 of lids opened to find the reward if birds search at random, calculated following [51]. By  
386 the second test trial (2 h after the probe and consolidation trials) the birds' search  
387 efficiency was better than the random expectation and remained so until the end of the  
388 experiment (see Table S1). Error bars give the 95% confidence interval, adjusted for  
389 within subjects repeated measures.

390 **Figure 2. The association between memory test performance and the number of**  
391 **fledglings and independent young produced per nest.** The mean memory  
392 performance (measured as the number of lids opened during test trials) associated with  
393 each level of nest success is shown for males in blue (A, C) and females in red (B, D).  
394 A smaller value (on the right of each x-axis) represents a more accurate performance in  
395 the memory test (i.e. fewer lids opened to retrieve mealworms during the experiment).  
396 Error bars give the standard error. The number of nests associated with each mean is  
397 shown above each point. As very few nests had 3 fledglings/independent young, these  
398 nests are grouped together with nests that had 2 fledglings/independent young. See  
399 Tables S2 and S3 for full multi-model averaging results for both males and females.

400 **Figure 3. The relationships between male memory performance and provisioning**  
401 **behaviour.** Males with superior memory performance fed their chick(s) a larger  
402 proportion of food that was equivalent to or larger than a mealworm in size (i.e. ~1.5 cm  
403 in length and 0.1 g in weight; A). The amount of time males spent flying per hour also  
404 decreased for males with superior spatial memory performance (B). See Table S4 for  
405 full multi-model average results for the behavioural observations of both males and  
406 females.

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**Deleted:** had increased provisioning

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**Deleted:** quality (A). Provisioning quality was defined as the proportion of sharing bouts where the amount delivered was



411 **Table S1. Comparison of actual search efficiency with the random search**  
412 **expectation. Related to Figure 1.**

413 **Table S2. The top models for each measure of reproductive success. Related to**  
414 **Figure 2.**

415 **Table S3. Multi-model average for the models of reproductive success. Related to**  
416 **Figure 2.**

417 **Table S4. The multi-model average for the models of foraging and provisioning**  
418 **behaviour. Related to Figure 3.**

419 **Table 1. The factors included in models of our measures of reproductive success**  
 420 **in the 2016 – 2017 breeding season.** Bird ID was specified as a random factor in all  
 421 GLMMs where the response was at the level of the nest (these models were also  
 422 weighted by clutch size). Models were run separately for males and females, as the  
 423 sample size was insufficient to analyse at the level of pairs.

Response	Variables included in the full model
Start date for the season* <i>Quasipoisson GLM</i>	parent cohort, paired last season, memory performance
Total clutches produced in season <i>Poisson GLM</i>	parent cohort, start date, parent survived entire season (Y/N), nest predation in season ('1' if at least one nest predation, '0' for no confirmed nest predation), memory performance
Chicks hatched per nest <i>Poisson GLMM</i>	parent cohort, start date, parent survived nesting† ('1' if survived until fledgling independence, '0' if not), sequence of the clutch within the season (e.g. 1, 2, 3; hereafter 'clutch number'), memory performance
Total fledglings per nest <i>Poisson GLMM</i>	parent cohort, start date, parent survived nesting†, clutch number, memory performance
Independent young per nest <i>Poisson GLMM</i>	parent cohort, start date, parent survived nesting†, clutch number, memory performance
Total independent young per season <i>Poisson GLM</i>	parent cohort, start date, parent survived entire season, nest predation in season, memory performance

424 \* We only examined individuals that started the season together (i.e. we excluded pairs  
 425 where the partner had already attempted to breed with another mate).

426 † Only included in the full models for males, as all females survived all nesting attempts  
 427 in the 2016/2017 breeding season.

## 428 STAR+METHODS

### 429 CONTACT FOR REAGENT AND RESOURCE SHARING

430 Further information and requests for resources and reagents should be directed to and  
431 will be fulfilled by the Lead Contact, Rachael Shaw ([rachael.shaw@vuw.ac.nz](mailto:rachael.shaw@vuw.ac.nz)).

### 432 EXPERIMENTAL MODEL AND SUBJECT DETAILS

433 The North Island robin (*Petroica longipes*; here we use their Māori name, toutouwai)  
434 study population is located within a 25 hectare area at Zealandia Wildlife Sanctuary in  
435 Wellington, New Zealand (the site is described in more detail elsewhere [27]). Since  
436 2014 all birds holding territories or hatched within the study site have been banded with  
437 a unique combination of three leg band colours for individual identification. We have  
438 monitored resident adult birds at our study site since 2014. In the 2016/2017 season the  
439 median age of breeding birds was 3 years, with a range of 1-10 years ( $N_{males} = 40$ ,  
440  $N_{females} = 32$ ). Toutouwai may successfully nest up to three times per season, with the  
441 first clutch typically containing 2 eggs and later clutches 2 – 3 eggs [30,39]. Chicks  
442 fledge at around 21 days old and both parents provision offspring from hatching through  
443 to independence (defined as juveniles surviving until at least 4.5 weeks post-fledge,  
444 which is when young independently forage and may begin dispersing [39]). This  
445 research was approved by Victoria University of Wellington's Animal Ethics Committee  
446 and carried out under permit from New Zealand's Department of Conservation  
447 (Authorisation number: 38497-FAU).

### 448 METHOD DETAILS

#### 449 Memory test

450 In the winter (6th June 2016 – 29th June 2016) we gave a memory test to 63 ( $N_{male} =$   
451 36,  $N_{female} = 27$ ) toutouwai. The test apparatus was a grey plastic ring (outer diameter =  
452 40 cm, inner diameter = 30 cm, height = 1.5 cm) with eight wells (width = 1.5 cm, depth  
453 = 1 cm) evenly spaced around the circumference. Each well was covered with a white  
454 plastic lid that was held in place with a screw and could be swivelled open (Figure 1A).  
455 All individuals had previously learned how to open these lids [28]. We chose a test  
456 location on a bird's winter territory that was at least 5 m from the nearest neighbour  
457 (territory boundaries were identified by observing boundary displays between  
458 neighbours). Trials were only conducted when no conspecific intruders were present  
459 (including mates, as toutouwai pairs typically maintain separate territories in winter  
460 [52]). The apparatus was placed on a cleared, flat area that was ca. 10cm from a single  
461 tree (minimum diameter of 6 cm). The tree was used as a landmark to ensure that the  
462 orientation and location of the apparatus, as well as the position of the mealworm  
463 reward, were consistent across all trials. In every trial the eight well lids were fully  
464 closed. The location of the mealworm (relative to the landmark tree) was randomised  
465 between birds, but was consistent across all trials for each individual.

466 We conducted trials between 8:30 and 14:30. We began with a probe trial in  
467 which we allowed a bird to open all lids to search for the mealworm. At the start of the  
468 probe trial we placed a single mealworm on the forest floor in the centre of the  
469 apparatus (to ensure that every bird would begin a trial from the centre). After a bird  
470 took this mealworm we gave it 6 min to open all lids. If the bird did not open all lids  
471 within 6 min, we opened the remaining closed lids slightly (1 mm) and gave the bird an  
472 additional 3 min to open these lids, before removing the apparatus. All birds completed  
473 the probe trial. We began a consolidation trial 2 min after the probe trial had ended. At  
474 the start of the consolidation trial we threw a small (< 2cm) stick into the centre of the

475 apparatus; toutouwai typically followed the stick and thus began the trial in the centre of  
476 the apparatus. We gave birds up to 3 min to find the mealworm. The apparatus was  
477 removed once the toutouwai had retrieved the mealworm. Following the consolidation  
478 trial, we gave a bird five more trials that day, with trials spaced 1 h apart. Each trial  
479 followed the same procedures as the consolidation trial. The final trial (5 h after the  
480 consolidation trial) served as a control. In this trial no mealworm was present in the  
481 apparatus to control for the possibility that birds relied on non-spatial cues (e.g.  
482 olfactory cues, or subtle visual cues indicating the presence of the mealworm) to locate  
483 the hidden mealworm. To check motivation and weight, all toutouwai hopped on  
484 electronic scales to retrieve a mealworm before the first probe trial and after the final  
485 control trial. All birds took both worms.

#### 486 **Breeding season monitoring and foraging observations**

487 We monitored the breeding success of resident pairs at our study site following  
488 established protocols [30]. In the 2016/2017 breeding season we monitored 32 of the  
489 males and 19 of the females that had participated in the memory test. One pair never  
490 nested and so could not be included in analyses. Four male and eight female subjects  
491 disappeared prior to the breeding season (and were assumed to have either died or  
492 dispersed). Females that remained in the study area during the breeding season did not  
493 differ in terms of memory performance compared to those that either died or dispersed  
494 prior to breeding (Mann-Whitney U test:  $N_{stayed} = 19$ ;  $N_{dispersed} = 8$ ,  $W = 96.5$ ,  $P = 0.29$ ).  
495 We also mapped pairs' territories by using a Garmin® GPSMAP 62c to mark  
496 boundaries. Boundaries were found by observing territorial disputes, noting individuals'  
497 refusal to approach and take mealworms from the ground, or by the presence of  
498 geographic boundaries (large bodies of water or open spaces). We recorded at least

499 eight GPS points on the territory boundary for each pair. ArcMap® was used to create  
500 territory polygons from these points and obtain area estimates.

501 In the 2016/2017 breeding season we conducted behavioural observations for 25  
502 pairs when they were caring for the first clutch of the season with chick(s) that survived  
503 to 15 – 16 days post hatching. This observation timing was chosen to ensure that  
504 chicks were capable of thermoregulation, so that females were not overly constrained in  
505 terms of the time they could spend away from the nest, and that the breeding stage and  
506 testing conditions were as comparable as possible across pairs. Within these pairs, 18  
507 males and 14 females had participated in the spatial memory experiment. Observations  
508 occurred on days with wind speed <40kph and without heavy rain and were preceded  
509 by 15 min habituation time after the observer (R.D.M.) arrived on the territory. Each  
510 parent was observed for 1 h; the order (male or female first) was determined by a coin  
511 toss. The first observation began by 0830 and the second by 1000. The observer was  
512 positioned with a view of the nest and as much of the territory as possible and  
513 minimised their movement during the observation. If a bird moved out of visual range it  
514 was followed only to the point that the nest still remained in view. All prey acquisition  
515 and food sharing events were recorded. Prey size was recorded as smaller, equivalent  
516 to, or larger than a mealworm (which are typically ca. 1.5 cm in length and 0.1 g in  
517 weight). We used these size categories to estimate the mass of food delivered to each  
518 chick during the observation. We estimated that provisioning bouts equivalent in size to  
519 a mealworm provided 0.1g of food; sharing bouts that were larger were conservatively  
520 estimated to contain 0.15 g of food, and smaller bouts 0.05 g of food. We divided the  
521 summed mass of all sharing bouts by the number of chicks in the nest to estimate the  
522 total prey mass delivered to each chick per hour. The observer had extensive prior  
523 experience monitoring and feeding mealworms to robins but was naïve to individual's

524 memory performance scores. Data were scored in the field using the app ATracker  
525 Pro®.

## 526 **QUANTIFICATION AND STATISTICAL ANALYSIS**

527 All analyses were conducted in R (v. 3.1.1). We first investigated the birds' performance  
528 as a group in the spatial memory experiment. We calculated search efficiency as the  
529 number of lids an individual opened to find the mealworm (e.g. if a bird found the food  
530 under the third lid it opened, its search efficiency was 3 for that trial). To examine  
531 whether search efficiency improved over the spatial memory trials (excluding the  
532 consolidation and control trials), we ran a generalized linear mixed model (GLMM, using  
533 the *lme4* package in R) with a Poisson error structure and log link, including trial  
534 number as a fixed factor and individual as a random factor. We also compared the  
535 birds' actual search efficiency to a 'sampling without replacement' random search  
536 strategy (i.e. once a lid was open, a bird could not re-open it; calculated using equation  
537 8 in [51]). We used a two-tailed, one-sample Wilcoxon sign ranks test to evaluate  
538 whether the actual search efficiency was better than the random search expectation in  
539 each trial (reported in Table S1). In addition, we examined whether an individual's  
540 performance was repeatable across the four test trials (i.e., trials on hours 1-4,  
541 excluding the initial probe, consolidation and control trial). We used the package 'rptR'  
542 to implement a mixed-effect model approach with a poisson error structure to estimate  
543 the repeatability, adjusted for trial order [33]. Finally, we tested whether non-cognitive  
544 factors affected birds' spatial memory performance. Following previous studies of avian  
545 spatial learning [35,36], performance was the summed search efficiency, measured as  
546 lids opened to find the food reward, of the test trials (i.e. trials on hours 1-4). We used a  
547 Generalised Linear Model (GLM) with a Quasipoisson error distribution (as a Poisson  
548 error structure with a logarithmic link yielded overdispersion) to examine whether

549 performance was affected by body condition (calculated as body mass divided by  
550 tarsus length [28]), sex and banding cohort (used as a proxy for age, as not all  
551 individuals were of known age). We calculated an individual's average body mass from  
552 each reliable scale reading. We used profile likelihood to calculate the 95% confidence  
553 intervals (CI) for the fixed factors included in these models.

554         For the reproductive success measures we examined 'start date', which was  
555 defined as the date that incubation began for a pair (the first pair to breed in the study  
556 population had a start date of 0, the start date for subsequent pairs was the number of  
557 calendar days that had elapsed relative to this baseline, i.e. a pair that began incubation  
558 two weeks later had a start date of '14'), the total number of clutches produced in a  
559 season, the number of eggs hatched per clutch, the number of chicks fledged per nest,  
560 the number of independent young produced per nest and the total independent young  
561 produced in a season. We used a multi-model inference approach [37] to assess the  
562 relationship between winter memory performance in 2016 and subsequent reproductive  
563 success in the 2016/2017 breeding season, while controlling for other life history  
564 variables. We modelled the factors influencing our reproductive success measures  
565 using GLMs and GLMMs with a Poisson distribution and log link (with the exception of  
566 'start date', which was overdispersed and thus modelled with a Quasipoisson  
567 distribution, see Table 1). For each response variable we ran all possible combinations  
568 of the predictors outlined in Table 1. For each model in the resulting set we calculated  
569 the Akaike information criterion corrected for small samples sizes AICc (for Poisson  
570 models), or quasi-AICc (QAICc, for Quasipoisson models), as well as the change in AIC  
571 relative to the best model in a set ( $\Delta AICc$ /  $\Delta QAICc$ ) and the Akiake weight (AICw),  
572 which gives the conditional probability of the model [37,38]. In Table S3 we report these  
573 measures. We obtained averages of model parameters by averaging across the full



574 model set (as is recommended best practice [38]). We used profile likelihood to  
575 calculate the 95% CI for the averaged predictor variables. The average models for each  
576 reproductive measure are reported in Table S4. For all our analyses we examined the  
577 sexes separately, as sample sizes were insufficient to analyse at the level of pairs. We  
578 also tested the correlation between 2016/2017 breeding territory size (measured in m<sup>2</sup>)  
579 and memory performance using Spearman rank correlations.

580 Finally, we examined parental foraging and provisioning behaviour. We used a  
581 multi-model inference approach (as described above) to investigate the factors affecting  
582 four measures of foraging and provisioning behaviour: foraging rate (items acquired per  
583 minute spent foraging), provisioning quantity (estimated mass of food delivered to a  
584 chick per hour), the proportion of large items shared (the proportion of sharing bouts in  
585 which the items shared were equivalent to or larger than a mealworm) and the amount  
586 of time spent flying during the observation. We used linear models (LM) to examine the  
587 influence of spatial memory performance and the number of chicks in the nest on the  
588 foraging rate (log transformed). We used LMs to examine the influence of foraging  
589 duration (min spent foraging in the hour), memory performance, the amount eaten by  
590 the parent and the flying duration on provisioning quantity. We examined the proportion  
591 of large items shared using a binomial GLM, with the number of mealworm sized or  
592 larger items out of the total items shared as the response, and memory performance,  
593 the number of chicks in the nest and the provisioning rate (no. of sharing trips made per  
594 min spent foraging) as predictors. Finally, we used a LM to examine how memory  
595 performance, provisioning rate and the proportion of large items shared influenced  
596 flying duration. We ran separate models for the two sexes and used profile likelihood  
597 (LM) and bootstrapping (binomial GLM) to calculate 95% CI for the averaged model

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601 parameters. The model averaging results for these models and their parameters are  
602 reported in Table S4.

603 **Data availability.** The data that support the findings of this study are included as  
604 supplementary datasets 1-3.